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Weed seed bank emergence across the Corn Belt

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Even casual observers of weeds have noticed that certain annual species are abundant in some years and less common in other years. Although reasons for this phenomenon are uncertain, many hypotheses could explain these observations. Explanations for differential abundance from one year to the next might include annual variation in crop type, time of seedbed tillage, previous year's seed production, herbicide efficacy, pathogen attack, and insect consumption. Another possible explanation involves "emergence percentage," the percentage of a weed's seedbank that emerges as seedlings each year. Emergence percentages often differ among species and, at least in some instances, also vary annually within a species (Roberts and Ricketts 1979; Stoller and Wax 1973). Emergence percentage may be high in one year because most seeds lack dormancy, but low in another year because seed dormancy was maintained or induced, for instance, by a specific weather condition or event. To test this latter hypothesis, knowledge of a weed's emergence percentages over a series of years or sites would be necessary.

Emergence percentage is interesting not only from a natural history perspective, but also because it is a critical variable for predicting the population dynamics of annual weeds (Mortimer et al. 1989). Despite the recognized importance

Field experiments, conducted from 1991 to 1994, generated information on weed seedbank emergence for 22 site-years from Ohio to Colorado and Minnesota to Missouri. Early spring seedbank densities were estimated through direct extraction of viable seeds from soil cores. Emerged seedlings were recorded periodically, as were daily values for air and soil temperature, and precipitation. Percentages of weed seedbanks that emerged as seedlings were calculated from seedbank and seedling data for each species, and relationships between seedbank emergence and microclimatic variables were sought. Fifteen species were found in 3 or more site-years. Average emergence percentages (and coefficients of variation) of these species were as follows: giant foxtail, 31.2 (84%); velvetleaf, 28.2 (66); kochia, 25.7 (79); Pennsylvania smartweed, 25.1 (65); common purslane, 15.4 (135); common ragweed, 15.0 (110); green foxtail, 8.5 (72); wild proso millet, 6.6 (104); hairy nightshade, 5.2 (62); common sunflower, 5.0 (26); yellow foxtail, 3.4 (67); pigweed species, 3.3 (103); common lambsquarters, 2.7 (111); wild buckwheat, 2.5 (63), and prostrate knotweed, 0.6 (79). Variation among site-years, for some species, could be attributed to microclimate variables thought to induce secondary dormancy in spring. For example, total seasonal emergence percentage of giant foxtail was related positively to the 1st date at which average daily soil temperature at 5 to 10 cm soil depth reached 16 C. Thus, if soil warmed before mid April, secondary dormancy was induced and few seedlings emerged, whereas many seedlings emerged if soil remained cool until June.

Nomenclature: Common lambsquarters, *Chenopodium album* L. CHEAL; common purslane, *Portulaca oleracea* L. POROL; common ragweed, *Ambrosia artemisiifolia* L. AMBEL; common sunflower, *Helianthus annuus* L. HELAN; giant foxtail, *Setaria faberi* Herrm. SETFA; green foxtail, *Setaria viridis* (L.) Beauv. SETVI; hairy nightshade, *Solanum sarrachoides* Sendtner SOLSA; kochia, *Kochia scoparia* (L.) Schrad. KCHSC; pigweed species, *Amaranthus* spp.; Pennsylvania smartweed, *Polygonum pennsylvanicum* L. POLPY; wild-proso millet, *Panicum miliaceum* L. PANMI; prostrate knotweed, *Polygonum aviculare* L. POLAV; velvetleaf, *Abutilon theophrasti* Medik. ABUTH; wild buckwheat, *Polygonum convolvulus* L. POLCO; yellow foxtail, *Setaria glauca* (L.) Beauv. SETLU.

Key words: Emergence prediction, seed dormancy, weed seeds, weed seedlings.

of emergence percentage, it has been treated as a static variable in most models of weed population dynamics (Cousens and Mortimer 1995; Melander 1993). That is, emergence percentage has been considered to be a rate variable that changes for different species, but not from one year to the next within a species. Accordingly, in these models the percentage of a species' seedbank that emerges as seedlings will be the same (e.g., 20% for sterile oat, *Avena sterilis* L. [Gonzalez-Andujar and Perry 1995]) regardless of potentially large yearly differences in weather during various seasons that could influence the behavior of the weed species. We do not criticize the use of static emergence percentages, as they represent the state of the art of weed population modeling. Instead, we suggest that as our understanding of the population ecology of weed seedbanks increases, dynamic emergence percentages should replace their static counterparts.

Emergence percentages are also important for investigations of economically based weed management decision aids (Lybecker et al. 1994; Swinton and King 1994). These decision aids project potential weed pressure based, in part, upon emergence percentages. If annual emergence percentages for some species vary appreciably and predictably, then

decision aids could be modified accordingly, allowing for improved efficiency in weed management (Forcella et al. 1996). A hypothetical example follows.

An annual grass and an annual broadleaf weed coexist at moderate densities in the same field. Both species have similar average annual emergence percentages, but each has a unique response (secondary dormancy) to microclimate prior to germination in spring or early summer. In an average year, both species would emerge at densities that require application of two herbicides, one specific to grasses and the other specific to broadleaf weeds. In contrast, spring weather during one year might induce secondary dormancy in the grass, resulting in high broadleaf populations relative to that of the grass. Timely prediction of the high broadleaf and low grass populations in the latter instance would permit fine-tuning of weed management, i.e., apply the broadleaf herbicide, but delay decision on grass control until some time after crop emergence, when grass infestation levels can be assessed. Although these decisions would achieve maximum efficiency where exact weed seedbank densities are known, they could also be used effectively when only relative ratings of weed density are known from the previous year. This latter type of information is commonly used by weed managers. To date, unfortunately, weed managers do not have a priori knowledge of forthcoming emergence percentages.

Emergence percentage may be governed by a species' sensitivity to induction of secondary dormancy. For summer annual weeds, this sensitivity is probably expressed sometime prior to potential germination in spring or summer, and it is likely governed by soil microclimate (Egley 1995; Taylorson 1987). Temperature and water potential are known to regulate secondary dormancy of some summer annual weeds in laboratory environments. For example, Taylorson (1982) found that hydrated and non-dormant seeds of giant foxtail were induced into secondary dormancy when exposed to 35 C in the dark. When kept at this temperature for 0, 2, 4, 8, 24, 48, and 96 h, and then transferred to 20/30 C for 5 d, germination percentages were 56, 54, 57, 40, 19, 16, and 4, respectively. Thus, induction into secondary dormancy apparently was initiated between 8 to 24 h at 35 C. The relevance of this finding is that soil surface temperatures readily reach 35 C during spring in the Corn Belt (Gupta et al. 1983). Thus, these controlled laboratory results provide a clue to how field data can be analyzed with respect to seedbank emergence percentages and induced dormancy (Egley 1995). That is, these results suggest that single-day events may play large roles in determining annual emergence percentages of summer annual weeds.

The laboratory results for giant foxtail also provide a basis for conceptualizing the variation in annual emergence percentages for summer annual weeds. The concept is illustrated in Figure 1, using soil temperature as the hypothetical microclimate variable that causes induction into secondary dormancy. Other soil microclimate variables, such as water potential, carbon dioxide and oxygen concentrations, etc., could induce secondary dormancy (Simpson 1991; Taylorson 1987). Testing the hypothesis (Figure 1) with field data was an objective of this study. A necessary prerequisite objective was to document the variability of emergence percentages across sites and years for as many species as possible in the north central United States.

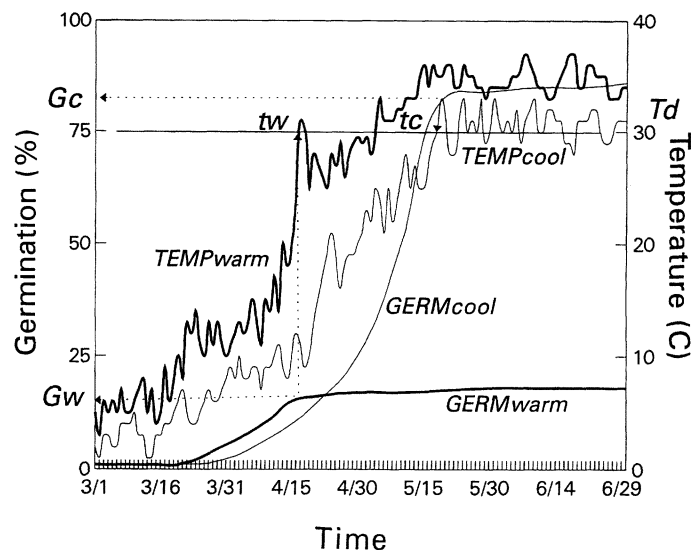


FIGURE 1. Hypothetical relationships among seed germination, soil temperature, and the temperature threshold that induces secondary dormancy in a summer annual weed. Temperature near the soil surface is represented by lines TEMP_{cool} (cool spring) and TEMP_{warm} (warm spring). The horizontal line extending from point T_d is the threshold temperature, 30 C, that induces secondary dormancy. Lines GERM_{cool} and GERM_{warm} represent cumulative seed germination in cool and warm years, respectively. In a cool year TEMP_{cool} rises above T_d at time t_c (May 15). A vertical line is drawn from t_c to where it intersects GERM_{cool} and from this point a horizontal line is drawn to the Y-axis. Relative germination or emergence percentage in cool years, G_c, is indicated where the horizontal line meets the Y-axis, which in this case is at about 85%. In contrast, in a warm year TEMP_{warm} intersects T_d at t_w. A vertical line from t_w meets the germination curve and is extended horizontally to G_w on the Y-axis. In this case, G_w is about 15%. Thus, in this hypothetical case, if soil temperature stayed low during spring, most of the seeds that were nondormant in early spring would germinate and emerge as seedlings. However, if soil temperature rose above the threshold in early spring, even if only for a single day, then secondary dormancy would be induced in the previously nondormant seeds. Consequently, germination would cease, and final emergence would be equivalent to whatever the germination percentage was prior to the date that soil temperature exceeded the threshold, about 15% emergence.

Materials and Methods

Experimental protocols closely followed those reported by Forcella et al. (1992), with the exception of some location differences. Experimental sites were located at federal or state agricultural experiment stations. The closest cities or weather stations and associated soil types were as follows: (1) Wooster, OH, Wooster silt loam, Typic Fragiudalf, fine, mixed, mesic; (2) Hickory Corners, MI, Kalamazoo sandy loam, Typic Hapludalf, fine-loamy, mixed, mesic; (3) Urbana, IL, Flanagan silt loam, Aquic Argiudoll, fine, montmorillonitic, mesic; (4) Arlington, WI, Plano silt loam, Typic Argiudoll, fine-silty, mixed, mesic; (5) Rosemount, MN, Waukegon silt loam, Typic Hapludoll, fine-silty over sandy, mixed, mesic; (6) Ames, IA, Nicolett loam, Aquic Hapludoll, fine-loamy, mixed, mesic; (7) Morris, MN, Barnes loam, Udic Pachic Haploboroll, fine mixed, mesic; (8) Columbia, MO, Mexico silt loam, Mollic Endoaqualf, fine, montmorillonitic, mesic; (9) Brookings, SD, Vienna loam, Udic Haploboroll, fine, loamy, mixed; (10) Scottsbluff, NE, Trip sandy loam, Aridic Haplustoll, coarse-silty, mixed, mesic; and (11) Akron, CO, Weld silt loam, Aridic Paleustoll, fine, montmorillonitic, mesic. All soils had been plowed the previous autumn and contained little surface residue.

Three to 4 plots were established at each site. Plots ranged

in size from 30 to 100 m². Twenty soil cores were collected from each plot in early spring. Soil cores ranged in diameter from 3 to 5 cm, depending upon the type of equipment available to the site investigator. They were 10 to 15 cm deep, the range representing the level of accuracy typically encountered when sampling wet soils in spring following autumn tillage. Weed seeds were extracted from each soil core independently, species identified, categorized as sound (whole or filled) or unsound (empty or hollow) seed, counted, and expressed on a m² basis. Seed extraction procedures varied by site and available equipment, ranging from elutriation (Gross and Renner 1989) to centrifugation (Buhler and Maxwell 1993) to wet sieving (Malone 1967). The different procedures were chosen for convenience. Based upon our collective experience with these methods, we believe that they may have affected the ease and speed with which samples were processed, but that they had no appreciable numerical influence on the results.

Permanent quadrats were established within each plot. Quadrat sizes ranged from 0.1 to 1.0 m², and the number of quadrats per plot ranged from 5 to 20, depending upon the equipment and labor available to each site investigator. Each quadrat was placed within 1 m of where 1 or more of the soil cores originated. Seedlings were counted and removed at least 3 times during the growing season so that the total cumulative seedling emergence could be calculated.

Both seedbank and seedling densities were calculated on a m² basis. Emergence percentages were calculated by dividing cumulative seedling density by the density of sound seeds within the seedbank for each species in each plot (replication) and year, and then multiplying by 100. The average among-plot emergence percentage and standard deviation were calculated for each species. There were instances in which a few seedlings of a species were recorded in a plot, but no seeds were detected in the associated seedbank. Data from these plots were excluded from calculations of emergence percentages. These situations arose only for species with very low densities at a specific site. In other instances, seedlings or seeds were found in some plots but not others. The latter plots were also excluded from calculations of average within-site emergence percentages. Consequently, for some species at some sites, there were too few replications and thus too little data to calculate standard deviations.

Weather data were obtained for each of the 22 site-years. Data included daily air temperature, soil temperature at a depth of 5 to 10 cm, and precipitation. Values for soil temperature on various days were occasionally missing in some data sets. When this occurred, a regression equation was calculated for simple linear correlations of air temperature and soil temperature for 10 d preceding and 10 d following the omission. The regression equation then was used to estimate the missing soil temperature values based on air temperature.

Weather data sets for all sites containing certain species, such as giant foxtail, were examined for the first day during which average daily soil temperature (at a depth of 5 to 10 cm) reached 10, 11, 12 . . . 20 C between April 1 and June 30. The maximum value of 20 C was chosen because average daily soil temperature at a depth of 5 to 10 cm rarely exceeds 20 C until July, at which time seedling emergence for most species is usually complete. Similarly, the 1st day during which soil (5 cm deep) water potential decreased to

specific levels was recorded for all data sets. These levels were as follows: -0.1, -0.2, -0.3, -0.4, -0.5, -0.6, -0.7, -0.8, -0.9, -1, -2, -3, -4, and -5 MPa (Megapascals). MPa was estimated based upon relationships among daily soil temperature, daily rainfall, and soil type (Forcella 1993).

Each temperature and water potential was considered a potential threshold correlate of a dormancy threshold. We use the term "threshold correlate" because our recordings of soil temperature (and estimated water potential) were based on temperature probes placed at 5 to 10 cm soil depth, which are the standard shallowest depths at which soil temperature is recorded at most weather stations. However, seeds of most weeds typically germinate and emerge only from the upper 2 to 3 cm of soil (Buhler 1995), where daily soil temperatures in spring can be much higher than those at 5 to 10 cm. Consequently, the actual temperature thresholds that induced dormancy were higher than those recorded at 5 to 10 cm, which were used for correlations in this study. The correlate was graphed against emergence percentage for each species with 3 or more site-years of data. Each graph was visually interpreted for the presence of a linear, curvilinear, or sigmoidal pattern. Where such a pattern within the data (1st date of threshold occurrence vs. emergence percentage) was observed, a best fit equation was generated through statistical software (Anonymous 1994). Where possible, a sigmoidal equation was chosen to match the presumed fundamental response of emergence percentage to an environmental threshold (Figure 1).

Because seeds of many small-seeded annual weeds germinate and emerge primarily from 0 to 2 cm soil depth (Buhler 1995), daily temperatures of these soil layers may be more important in regulating plant behavior than those at 5 to 10 cm soil depth. Daily maximum and minimum temperatures at the soil surface were estimated from air temperatures (Gupta et al. 1983). Soil temperatures at 1- and 2-cm soil depths were calculated based on estimated daily heat flux from the soil surface via a depth-specific normalized soil temperature procedure described by S.C. Gupta.¹ Temperature estimates for these shallow soil layers were compared to observed temperatures (5 to 10 cm deep).

Results and Discussion

Average Emergence Percentages Within Locations

Seedbank emergence data were collected for 28 weed species across 22 locations or years (site-years). Average emergence percentages and associated within-site coefficients of variation (CV) for each species are listed in the Appendix. Emergence percentages of species that dominated the sites where they occurred varied relatively little from one plot to the next within a site-year. For example, CV of emergence percentages for giant foxtail, velvetleaf, common ragweed, common cocklebur (*Xanthium strumarium* L.), and tall morningglory [*Ipomoea purpurea* (L.) Roth] were consistently less than 50%. In contrast, CV of emergence percentages for less dominant species often exceeded 75%. We attribute much of this differential variability to sampling error. The typically high level of within-site spatial variability of low-density weed populations likely results in greater error when combining two population measurements (i.e., seedling density divided by seedbank density) in comparison to high-density weed populations. This phenomenon can be illus-

TABLE 1. Emergence percentages of 15 weed species for which 3 or more site-years of data were collected.

Species	Average (%)	Minimum (%)	Maximum (%)	CV (%)	Site-years (no.)
Giant foxtail	31.2	9.1	100.0	84	8
Velvetleaf	28.2	9.3	53.5	66	3
Kochia	25.7	0.3	50.2	79	3
Pennsylvania smartweed	25.1	0.6	48.5	65	6
Common purslane	15.4	0	44.9	135	3
Common ragweed	15.0	0.1	38.2	110	3
Green foxtail	8.5	0	20.5	72	8
Wild proso millet	6.6	0.6	16.1	104	3
Hairy nightshade	5.2	1.3	9.3	62	3
Common sunflower	5.0	3.2	6.3	26	3
Yellow foxtail	3.4	0.3	5.6	67	3
Pigweed spp.	3.3	0.2	13.1	103	19
Common lambsquarters	2.7	0	10.1	111	17
Wild buckwheat	2.5	0.5	4.7	63	4
Prostrate knotweed	0.6	0	1.1	79	3

trated with any of several of our data sets. For example, common lambsquarters emergence percentages during 1991 and 1994 in Nebraska were associated with CVs of 98 and 20, respectively (Appendix). At this site, seedbank densities were relatively low and variable among plots during 1991 ($3,634 \pm 2,522$ seeds m^{-2}), whereas during 1994 the seedbank was much larger and more homogeneous ($9,480 \pm 1,366$ seeds m^{-2}).

We recognize that the unequal variances associated with the average emergence percentages of the many species and site-years within our data sets may result in statistical difficulties and potentially introduce error. Nevertheless, in subsequent analyses where we relate environmental variables to emergence percentages, we chose to ignore within-site variation and characterize each site-year for each species by its straightforward, arithmetic, within-site, average emergence percentage. Our rationale for this approach was that the averages represented a summary statistic for one or more subsamples (plots) from each site or field; and fields, not subsamples, were our intended conceptual units of study.

Average Emergence Percentages Across Locations

The average percentage of a seedbank that emerged annually varied greatly among species and among years within a species (Table 1). For species occurring at 3 or more sites, average emergence was highest for giant foxtail (31.2%), and lowest for prostrate knotweed (0.6%). Ranges of emergence percentages paralleled those for averages, with giant foxtail values ranging from 9.1 to 100% and those for prostrate knotweed ranging from 0 to 1.1% among site-years. Among-site variation (CV) of emergence percentage was greatest ($\geq 110\%$) for common lambsquarters, common purslane, and common ragweed, indicating substantial effect of year and site on the percentage of seedbanks that germinate and emerge. In contrast, CV values were lowest (62 to 67%) for hairy nightshade, Pennsylvania smartweed, velvetleaf, wild buckwheat, and yellow foxtail. For these species, variation in emergence percentages was still high, but apparently not as affected by year and site as the former species. The lowest CV (62%) underscored the fact that emergence percentage is a highly dynamic characteristic of these weed species.

Emergence percentages reported in the literature generally agree with those in Table 1. Emergence percentages of giant foxtail and common ragweed near Upland, Indiana, during 1989 were 55 and 42%, respectively, from the top 5 cm of soil that had been rototilled thoroughly to a 20-cm depth (Rothrock et al. 1993). Dividing these values by 2 would make them comparable to our data, which were calculated from 10-cm-deep soil cores. Thus, both corrected values (27.5% for giant foxtail and 21.0% for common ragweed) fall within the range of our observed values (Table 1). In Britain, Roberts (1963) reported seedbank and seedling densities for common lambsquarters in 4 tillage systems. Emergence percentages calculated from these values ranged from 4.8 to 5.9% for deeply plowed (> 36 cm) soils, and 6.5 to 9.0% for more shallowly plowed (< 18 cm) soils. Both sets of emergence values are within the range of our observations for common lambsquarters. Emergence percentages of seeds buried 5 cm deep in Illinois were 31 and 19% for velvetleaf and 4 and 42% for yellow foxtail during 1967 and 1969, respectively; and in 1969 they were 13% for common ragweed and 21% for Pennsylvania smartweed (Stoller and Wax 1973). Only the high value for yellow foxtail is out of the range of our data (Table 1).

Average emergence percentage (Table 1) could be used where better estimates are unknown. However, a substantial risk would be encountered when using average emergence percentage because of the high CVs. Where the need to avoid risks associated with underestimating emergence percentage and subsequent weed densities may be important, other emergence statistics could be used instead of average values. For example, average emergence percentage plus 1 standard deviation would result in an emergence statistic that would equal or exceed actual emergence percentages with a probability of 0.83. Maximum emergence percentages could be used when there is a paramount need to eliminate risks of underestimating weed densities.

The value of using these various emergence percentages can be demonstrated by applying them in bioeconomic weed management decision aids, such as WEEDSIM (Swin-ton and King 1994). We initialized WEEDSIM to make weed management recommendations for corn in rotation with a grain legume. Initialization parameters were as follows: maximum potential corn yield of 7 Mg ha^{-1} ; corn planting date of May 15; silt loam soil; grain and herbicide prices typical of 1994; and a giant foxtail seedbank of 1,000 seeds m^{-2} . However, we varied giant foxtail emergence percentages to correspond to those in Table 1: 9%, minimum value observed; 31%, mean; 57%, mean + one standard deviation (standard deviation can be calculated from Table 1 as follows: $Average \times CV/100$) and 100%, or the maximum value observed. Rotary hoeing was the most profitable weed-management recommendation, with an emergence percentage of 9%. With an emergence percentage of 31%, cyanazine (2-[[4-chloro-6-(ethylamino)-1,3,5-triazin-2-yl]amino]-2-methylpropanenitrile) at 3.3 kg ai/ ha^{-1} was recommended. In contrast, when emergence percentages were $\geq 57\%$, the most profitable decision was rotary hoeing plus cyanazine at 3.3 kg ai/ ha^{-1} . These variable recommendations reflect the fact that as emergence percentages increase, potential weed densities and weed pressure also rise, which, in turn, necessitates higher levels of weed management.

As the requirement for efficiency in weed management becomes more acute in the future, more accurate estimates of annual emergence percentages will be necessary. More accurate annual estimates can be derived for some species based upon an understanding of the environmental cues that govern secondary dormancy of their seeds.

Environmental Regulation of Emergence Percentage

Distinct linear patterns were apparent between first date of occurrence of specific soil temperatures or estimated water potentials and emergence percentages of some species. Where patterns were observed between emergence percentages and dates of microclimate occurrence, they typically arose only with one soil temperature (using intervals of 1 C) or one water potential (using intervals of 0.1 MPa). These specific soil temperatures or water potentials were considered to be the threshold correlates for induction of secondary dormancy for the species with which they were associated. They are described for individual species in the following sections. We have emphasized 6 species for which we obtained 4 or more site-years of data. For the remaining 9 species with 3 data sets (3 site-years) each, we only briefly mention possible thresholds and relevant literature.

Giant Foxtail

A distinct curvilinear relationship occurred between emergence percentages of giant foxtail and the 1st day that average daily soil temperature at 5 to 10 cm soil depth reached either 16 or 17 C (Figure 2a). Relationships between seedbank emergence percentages and first dates of occurrence of any temperature lower than 16 C or higher than 17 C appeared random. These results suggest that at the time soil (5 to 10 cm soil depth) reaches 16 to 17 C, conditions within the giant foxtail seedbank are appropriate for induction of secondary dormancy. Seeds that germinated before this time may result in emerged seedlings, but seeds that had not germinated by this time probably become dormant. The relatively small percentage of seedbanks that germinated and emerged at sites experiencing early incidences of 16 to 17 C soil temperatures may have arisen from (1) deeply buried seeds that escaped induction into secondary dormancy, (2) seed biotypes insensitive to secondary dormancy induced by high temperature, and (3) very early germinating seed biotypes.

Maximum daily air temperatures of about 26 C occurred at the time average soil temperatures at 5 to 10 cm soil depth reached 16 to 17 C. Estimated maximum soil temperatures (Gupta et al. 1983) at 0, 1, and 2 cm soil depths were about 33, 25 and 24, respectively, at this time. These shallow depths correspond to the soil depths from which most giant foxtail seeds germinate (Buhler 1995), and the associated surface temperature corresponds to that (35 C) known to induce secondary dormancy in giant foxtail under laboratory conditions (Taylorson 1982).

The proposed relationship between giant foxtail emergence percentage and the first-day soil temperature's exceeding 16 C was tested with independently derived data. Estimated emergence percentage of giant foxtail from the 0 to 10 cm deep soil zone at Upland, IN, in 1989 was 27.5% (Rothrock et al. 1993). We obtained weather data² for the

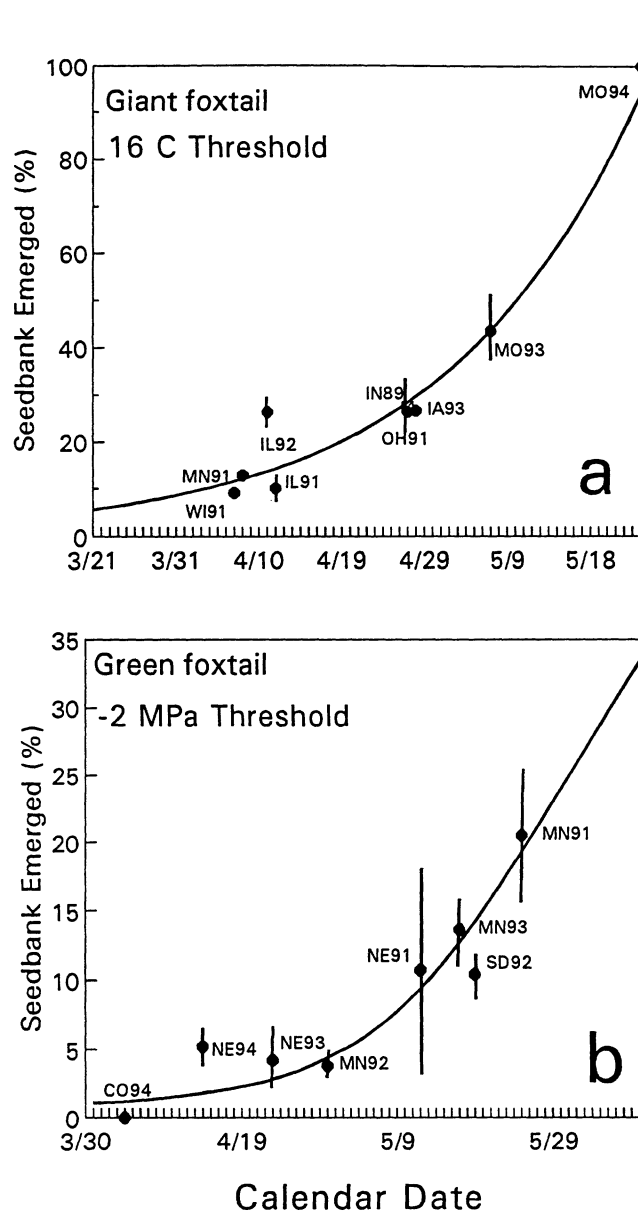


FIGURE 2. (a) Relationship between giant foxtail emergence percentages (E) and the first day (D) in spring that soil temperature (5 to 10 cm soil depth) reached 16 C. Data are from 8 site-years throughout the Corn Belt. Within the bounds of the data, the equation that describes the relationship is: $E = \exp(0.707 + 0.00019 \cdot D^2)$. The IN89 value was independently derived (Rothrock et al. 1993) and was not used in the analysis. (b) Relationship between green foxtail emergence percentages and the 1st day in spring that estimated water potential at 5 cm soil depth reached -2 MPa from 8 site-years throughout the Corn Belt. Within the bounds of the data, the equation that describes the relationship is: $E = [0.82 + 6.47 \cdot (1 / (1 + \exp(-(D - 141.71) / 15.38)))^2]$. Individual values are identified by state-year abbreviations; e.g., MO93 represents the value for Missouri in 1993. Bars represent 1 standard deviation and indicate within-site variability for each average emergence percentage. Bars were not available or are too small to be visible for some sites.

official weather stations closest to Upland. These data included air temperatures for Marion, IN (16 km west of Upland), and soil temperatures at 10 cm soil depth for Tipton, IN (46 km west of Upland). We used the air temperatures from Marion to simulate (Gupta et al. 1983) soil temperatures at 10 cm soil depth. Both measured and simulated soil temperatures first exceeded 16 C on April 27. When the date of April 27 and the emergence percentage

of 27.5% were plotted in Figure 2a, the resulting coordinate was closely associated with the proposed equation that described the relationship for emergence percentage and the dormancy-inducing soil temperature correlate for giant foxtail.

Within-site variability of emergence percentages for giant foxtail, as expressed by the standard deviation of the mean value for emergence percentage, was relatively low. Examples of these within-site standard deviations for giant foxtail are shown in Figure 2a.

Green Foxtail

Green foxtail emergence percentages were not highly correlated with soil temperature thresholds. For this species, unlike giant foxtail, only a small amount of variability in emergence percentages could be attributed ($r^2 = 0.28$, $P < 0.05$) to date of first occurrence of 16 C soil temperatures (data not shown). Other possible soil temperature thresholds explained even less variation in emergence percentages of green foxtail. Soil water potential appeared to regulate emergence percentage of green foxtail (Figure 2b). A sigmoidal relationship occurred between green foxtail emergence percentages and the date at which soil water potential (5 to 10 cm soil depth) first decreased below -2 MPa. This relationship explained 88% of the observed variation in emergence percentage.

Wild Buckwheat

A distinct relationship was apparent between the percentages of wild buckwheat seedbanks that emerged and the first day that average daily soil temperature at 5 to 10 cm soil depth reached 11 to 13 C (Figure 3a). There was no relationship between seedbank emergence and any temperature lower than 11 C or higher than 13 C. These results suggest that wild buckwheat has a lower threshold for induction into secondary dormancy than does giant foxtail. This prospect is reinforced by the observation that seedlings of wild buckwheat emerge earlier in spring than those of foxtails (data not shown). Similarly, in Michigan, wild buckwheat is not a problem where soils are tilled in May after the soil has warmed; it is a problem only in sugarbeet (*Beta vulgaris* L.) fields, where soil is tilled by April 15 and is still cold (K. A. Renner, unpublished data).

Pennsylvania Smartweed

The relationship between Pennsylvania smartweed emergence percentages and the 1st day that average daily soil temperature reached 10 C (Figure 3b) was less distinct than that for wild buckwheat. Nevertheless, it explained 75% of the observed variation. The validity of this relationship was tested with independently derived data. Seeds of Pennsylvania smartweed were buried in silt loam at 1.3, 2.5, 5.1, and 10.2 cm soil depths during autumn 1968 at Urbana, Illinois. Emergence percentages from these artificial seedbanks during 1969 were 19, 23, 21, and 1%, respectively (Stoller and Wax 1973). Average emergence percentage across all depths was 16%, and that for the upper 3 depths was 21%. The 1st day in 1969 at which average daily soil temperature at 10 cm soil depth exceeded 10 C was April

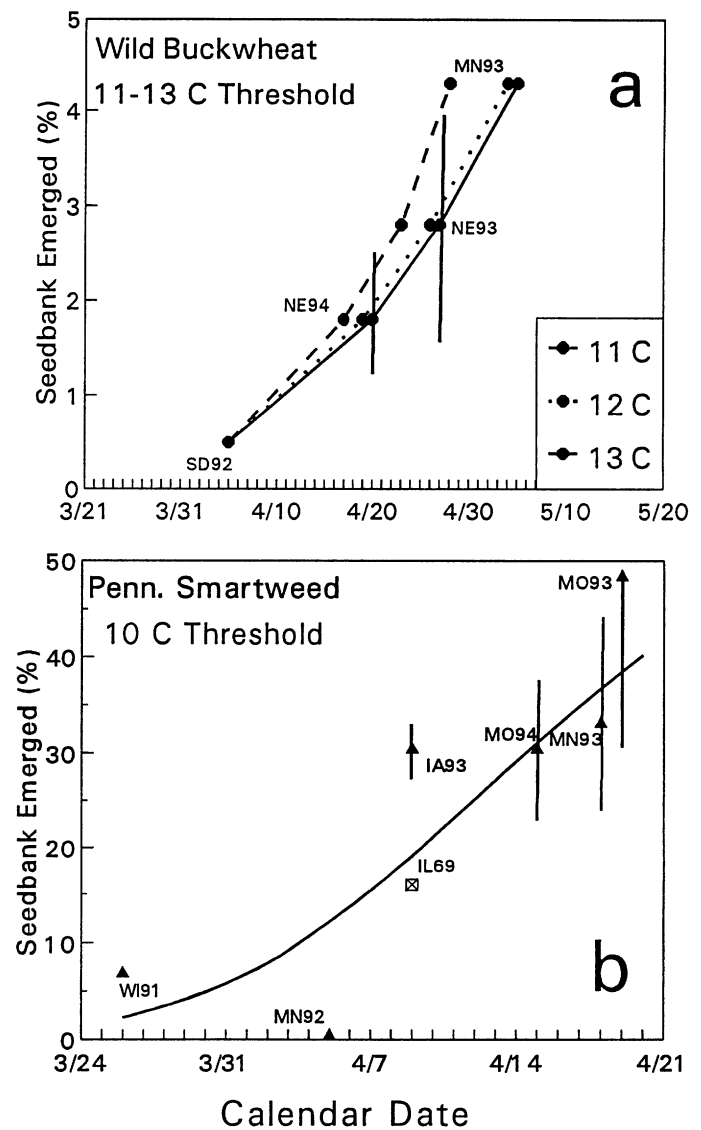


FIGURE 3. (a) Relationship between wild buckwheat emergence percentages (E) and the 1st day (D) in spring that soil temperature at 5 to 10 cm soil depth reached 11, 12, or 13 C from 4 site-years in the Corn Belt. Equation that best describes the relationship at the 13 C threshold is: $E = (-1.785 + 0.00027 \cdot D^2)^2$. (b) Relationship between Pennsylvania smartweed emergence percentages and the 1st day in spring that temperature at 5 to 10 cm soil depth reached 10 C from 6 site-years throughout the Corn Belt. Within the bounds of the data, the equation that describes the relationship is: $E = [-0.38 + 8.19 \cdot (1/(1 + \exp(-(D - 96)/(9.12))))]^2$. The IL69 value was independently derived (Stoller and Wax 1973) and was not used in the analysis. Individual values are identified by state-year abbreviations; e.g., MN93 represents the value for Minnesota in 1993. Bars represent 1 standard deviation and indicate within-site variability for each average emergence percentage. Bars were not available or are too small to be visible for some sites.

9 (Stoller and Wax 1973). Insertion of these data (April 9, 16%) into Figure 3b indicated a close relationship between predicted and independently observed emergence percentages.

Unfortunately, controlled laboratory data regarding induction into secondary dormancy are lacking for wild buckwheat and Pennsylvania smartweed. Low temperatures (2 to 10 C for 2 mo) are required for breaking dormancy of wild buckwheat seeds (Metzger 1991), as is true for other *Polygonum* species. Annual cycling of dormancy release in late

winter or early spring and dormancy induction in late spring or early summer, which occurs in related species (ladythumb, *P. persicaria* L.; prostrate knotweed; and *Rumex* spp., docks) (Courtney 1968; Karssen 1980/81; Totterdell and Roberts 1979), probably occurs in wild buckwheat and Pennsylvania smartweed. Such cycling would suggest existence of a springtime temperature threshold for secondary dormancy in wild buckwheat.

Common Lambsquarters

The microclimate threshold variable that accounted for most variation of emergence percentages of common lambsquarters was soil temperature at 16 C. The relationship was log-linear (Figure 4a), but not strong, with only 26% of the observed variability ($P < 0.05$) being attributed to the threshold temperature. Nevertheless, the relationship may have some validity based on greenhouse and laboratory investigations. Common lambsquarters seeds kept in darkness in a Kentucky greenhouse lacking temperature regulation apparently were induced into secondary dormancy during May (Baskin and Baskin 1977a). Light exposure tended to prolong non-dormancy, but by June most light-exposed seeds were also dormant. Common lambsquarters buried in field soil in the Netherlands and periodically retrieved for germination tests in the laboratory entered secondary dormancy at the same time soil temperature at a depth of 10 cm rose to about 15 C (Boumeester and Karssen 1993). In these experiments, however, secondary dormancy could be alleviated by laboratory exposure of seeds to nitrate, light, water, stress, and various temperature regimes, underscoring the fact that secondary dormancy for some species is a complex process (Baskin and Baskin 1977b). In the related species, perennial goosefoot (*Chenopodium bonus-henricus* L.), laboratory studies indicated that dark exposure of hydrated and nondormant seeds to 29 C for 4 d induced secondary dormancy (Kahn and Karssen 1980). Exposure of seed to water potentials of -0.86 MPa also induced secondary dormancy in this species, but the intensity of the response was not as great as with high temperature. Exposure of seeds to light negated any effects of high temperature or low water potential. These effects of light and dark on dormancy may explain some of the variability observed for common lambsquarters emergence percentages in our study. However, all of our sites were plowed, so most common lambsquarters seed probably would have been buried (Buhler 1995) and shielded from light, except, perhaps, during secondary tillage in spring.

Redroot pigweed (*Amaranthus retroflexus* L.) and other pigweeds

Non-dormant redroot pigweed seeds kept in a Kentucky greenhouse lacking temperature regulation apparently could not be induced into secondary dormancy (Baskin and Baskin 1977a). Similarly, in our study there were no obvious soil temperature thresholds for induction of secondary dormancy of pigweed. However, a poor relationship was found between the percentages of pigweed seeds that emerged and the 1st day that daily soil water potential decreased to -0.5 MPa (Figure 4b). There was no relationship between pigweed seedbank emergence and any water potential lower or

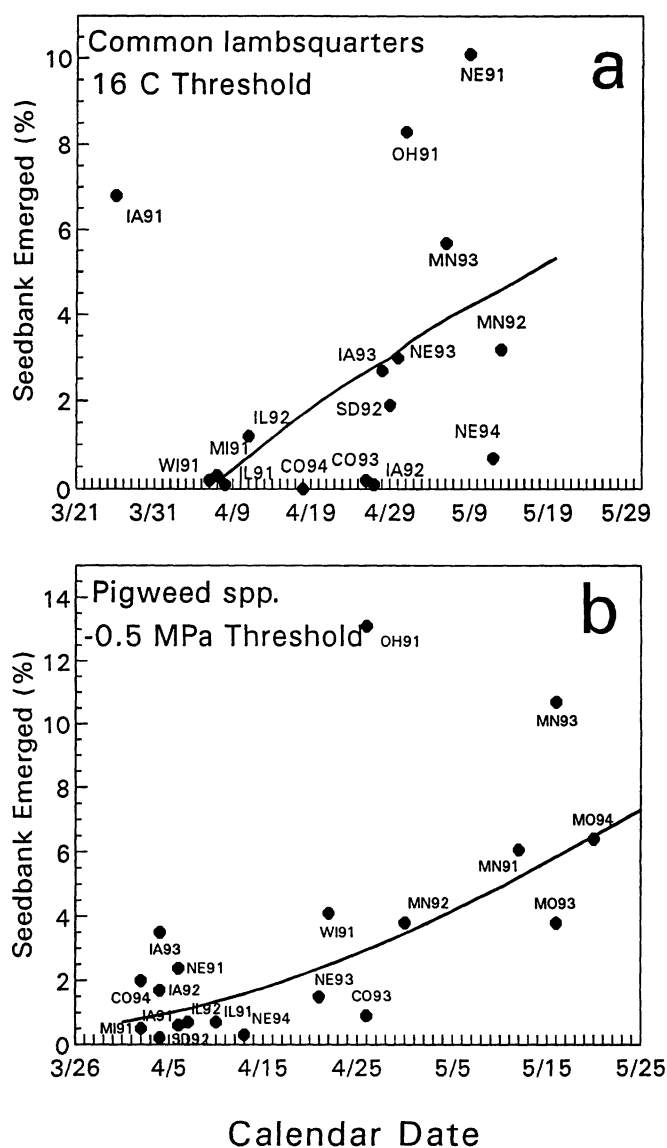


FIGURE 4. (a) Relationship between common lambsquarters emergence percentages (E) and the 1st day (D) in spring that soil temperature at 5 to 10 cm solid depth reached 16 C across 15 site-years throughout the Corn Belt. Within the bounds of the data, the equation that describes the relationship is: $E = (-64.63 + 14.16 \ln(D))$. The value for IA91 was considered an outlier and excluded from the analysis. (b) Relationship between pigweed species emergence percentages and the first day in spring that estimated water potential reached -0.5 MPa at 5 cm soil depth across 20 site-years throughout the Corn Belt. Within the bounds of the data, the equation that describes the relationship is: $E = [-0.65 + 4.78 \cdot (1/(1 + \exp(-(D - 116.55)/33.33)))]^2$. The value for OH91 was considered an outlier and excluded from the analysis. Individual values are identified by state-year abbreviations; e.g., NE93 represents the value for Nebraska in 1993. Error bars were not included in graphs to retain visual clarity; within-site variability can be ascertained by inspection of the Appendix.

higher than -0.5 MPa. These results are speculative, however, because the pigweed data sets from the different sites were comprised of various pigweed species, which may vary in regard to induced dormancy mechanisms. Although we believe redroot pigweed was the predominate species, other species may have included prostrate pigweed (*Amaranthus blitoides* S. Wats.), smooth pigweed (*A. hybridus* L.), and possibly others. Distinguishing pigweed species by visual seed and cotyledonary-stage seedling characteristics is difficult.

TABLE 2. Relationships among hypothetical daily minimum and maximum air temperatures in spring and simulated daily minimum and maximum soil temperatures at different depths in a moldboard-plowed silt loam soil whose residue was incorporated. Based on equations in Gupta et al. (1983). Air temperature values and ranges are based on those commonly observed in the Corn Belt in spring.

Air		Soil depth									
		0 cm		1 cm		2 cm		5 cm		10 cm	
		Temperature		Temperature		Temperature		Temperature		Temperature	
Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
0	15	1.9	16.7	4.4	15.4	4.7	14.1	5.4	12.2	6.2	10.8
5	15	4.5	16.7	5.1	15.5	5.4	14.2	6.0	12.5	6.8	11.1
5	20	4.5	24.3	5.5	22.7	6.1	20.5	7.1	17.6	8.3	15.5
10	20	9.7	24.3	10.4	23.3	10.8	21.7	11.6	19.5	12.5	17.9
5	25	4.5	31.7	5.9	28.5	6.6	25.6	8.0	21.9	9.6	19.0
10	25	9.7	31.7	10.8	29.1	11.4	26.8	12.5	23.7	13.8	21.4
15	25	16.7	31.7	18.0	30.1	18.4	28.6	19.1	26.5	19.9	25.0
10	30	9.7	37.6	11.0	31.9	11.6	29.3	12.9	25.8	14.4	23.1
20	30	24.3	37.6	25.8	33.9	26.1	32.9	26.6	31.5	27.1	30.5

Other Species (Three Site-years of Data)

Common ragweed is one of the earliest emerging summer annual species (Stoller and Wax 1973). Possible soil temperature (5 to 10 cm soil depth) thresholds that induced secondary dormancy in this species were correspondingly low, 11 to 13 C. Emergence percentages and dates for 13 C soil temperatures for common ragweed were 0.1, 6.8, and 38.2%, and April 5, 6, and 8, for South Dakota in 1992, Michigan in 1991, and Ohio in 1991, respectively. The association between higher emergence percentages with later dates in April for initial soil warming to 13 C can also be seen in the literature: 19% emergence from the upper 10 cm of soil and April 10 during 1969 in Illinois (Stoller and Wax 1973), and 21% emergence and April 22 during 1989 in Indiana. Lastly, common ragweed was easily induced into secondary dormancy in April in an unheated Kentucky greenhouse (Baskin and Baskin 1977a) when mean monthly minimum and maximum air temperatures reached 10 and 25 C, respectively. Thus, the possible 11 to 13 C soil temperature (5 to 10 cm soil depth) threshold we observed for this species may have some justification.

For hairy nightshade, 17 to 18 C appeared to be the soil temperature (5 to 10 cm soil depth) threshold for inducing dormancy. Emergence percentages and dates for first incidence of 18 C soil temperature were 1.3, 6.1, and 9.3%, and May 10, May 14, and May 17 for 1991, 1993, and 1994, respectively, in Nebraska. Hairy nightshade is a very late-emerging summer annual weed because its seeds germinate only after soil temperature reaches 25 C. However, seeds are induced into secondary dormancy if exposed to 30 C before they have a chance to germinate (Roberts and Bodrell 1983). Thus, the possible 17 to 18 C soil threshold may have some validity because these values can be associated with surface temperatures of > 30 C and minimum/maximum air temperatures of only 10/25 and 15/25 C (Table 2).

The soil temperature (5 to 10 cm soil depth) threshold for inducing dormancy in common sunflower may have been 19 to 20 C, but only three data sets were available for analysis. Emergence percentages and dates for first incidence of 20 C soil temperature were 3.2, 5.5, and 6.3%; May 1, May 10, and June 1 for South Dakota in 1991 and Nebraska in 1991 and 1993, respectively. Seeds of cultivated

forms of sunflower can be induced into secondary dormancy by high temperature treatments of 1 d duration in the laboratory (Corbineau et al. 1988). However, in this experiment, the treatment temperature was high—45 C—and may not be relevant to field situations except on very hot summer days.

Prostrate knotweed is, perhaps, the 1st and most well-known weed species whose seedbank was shown to cycle into and out of dormancy in response to seasonally high and low soil temperatures (Courtney 1968). Our data suggest that 10 C (or less) is the soil temperature threshold correlate that induces secondary dormancy in prostrate knotweed. Soil temperatures first reached 10 C on March 26 (Nebraska 1993), March 26 (Wisconsin 1991), and April 17 (Nebraska 1994) and resulted in emergence percentages of 0, 0.6, and 1.1%, respectively. This prospective low temperature threshold agrees well with information in the literature (e.g., Courtney 1968).

A possible soil temperature (5 to 10 cm soil depth) threshold that may have induced dormancy in common purslane was 19 to 20 C, but only three data sets were available for analysis and no supporting documentation could be found in literature sources. No obvious microclimate thresholds were detected for kochia, yellow foxtail, or wild proso millet. In contrast, abundant literature exists for velvetleaf dormancy. However, secondary dormancy may not be relevant for this hard-seeded species (Taylorson 1987). Variation in annual emergence percentages for hard-seeded species may be due simply to scarification by tillage, microbial degradation of seed coats, or to environmental cues in spring that break dormancy rather than induce it.

Weed seed dormancy in general, and secondary dormancy in particular, are complex phenomena (Simpson 1991; Taylorson 1987). Some weed species, especially those with hard seeds (Taylorson 1987), may not exhibit secondary dormancy. Moreover, even for species with pronounced secondary dormancy, several environmental variables may interact to induce dormancy or restrict seedling emergence in other ways, e.g., tillage, light, phytochrome, and interference by earlier-emerging species (Taylorson 1987). Consequently, the single-factor thresholds that we observed for giant foxtail, green foxtail, Pennsylvania smartweed, wild buckwheat, common lambsquarters, and pigweeds should be viewed

with caution. Indeed, in preliminary studies (Forcella 1992; Forcella et al. 1992) we speculated that emergence percentages and secondary dormancy were governed by weather variables that spanned 10- to 30-d durations. We now view those data interpretations as naive, and we have little doubt that our current observations will also be modified as we learn more about the ecology of weed seedbanks. For example, Dekker et al. (1996) recently suggested that "germinative capacity" of giant foxtail may be regulated by 3 separate but interacting effects of whole seed, excised caryopses, and isolated embryos, each of which may be governed by differing environmental events. Lastly, superimposed upon these physiological complications for interpretation of emergence percentages is the error arising from sampling of seedbanks and seedling populations in natural field settings. Consequently, we prefer to think of our results as working hypotheses to be used as rules of thumb until they are superseded by a more thorough understanding of weed ecology. Despite these problems, however, we believe that we have made some progress on this topic.

Our regional study of weed seedbanks and seedling emergence showed that emergence percentages of summer annual weeds were not static from one year or site to the next. Instead, they changed annually. In fact, annual variation in emergence percentages often was quite large for most species. Furthermore, variation in annual emergence percentages for some species apparently occurred in response to environmental thresholds. For example, thresholds for giant foxtail and Pennsylvania smartweed were associated with soil temperatures, at depths of 5 to 10 cm, of 16 and 10 C, respectively. That is, when soil temperature first reached the threshold in spring or summer, secondary dormancy was induced, and little further germination occurred for that year. Independently derived data substantiated these observations.

These results help to explain the commonly observed annual variation in dominance of summer annual weeds in agricultural fields and elsewhere. Moreover, these results may guide weed biologists and developers of weed population and management models in determining correct ranges of values to use for annual emergence from seedbanks of several species. More accurate predictions of weed populations may be possible for species whose environmental thresholds were quantified and confirmed by laboratory tests, e.g., giant foxtail. These latter results may be especially applicable because giant foxtail is the most important grass weed in the Corn Belt.

Sources of Materials

¹ Depth-specific normalized soil temperature procedure, "Guide to estimate soil temperatures under various tillage and residue conditions for the Northern Corn Belt," S. C. Gupta, Department of Soil Science, University of Minnesota, St. Paul, MN 55108.

² Weather data, P. Phillips, Indiana State Climatology Office, 1150 Lilly Hall, Purdue University, West Lafayette, IN.

Acknowledgments

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of Wisconsin; and South Dakota State University. Minnesota Science Journal Series No. 22, 272.

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APPENDIX. Within-site seedbank emergence averages and coefficients of variability for 28 weed species.^a Missing values denoted by “—” and “na” indicate means from single plots. Abbreviations are for state and year; e.g., CO93 is Colorado during 1993.

Site	Common lambsquarters		Redroot pigweed		Giant foxtail		Green foxtail	
	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)
CO93	0.1	na	0.9	22	—	—	—	—
CO94	0	141	2.0	53	—	—	0	0
IA91	6.8	na	0.6	na	—	—	—	—
IA92	0.2	na	1.7	93	—	—	—	—
IA93	2.7	27	3.5	62	26.7	na	—	—
IL91	0.1	50	0.7	41	13.0	41	—	—
IL92	1.2	90	0.7	59	26.4	22	—	—
MI91	0.2	34	0.5	51	—	—	—	—
MN91	1.1	na	6.1	na	—	—	20.7	48
MN92	3.0	52	3.8	87	—	—	3.8	23
MN93	5.7	64	10.7	97	—	—	13.6	37
Mn91	—	—	—	—	10.1	10	—	—
MO93	—	—	3.8	51	43.5	21	—	—
MO94	—	—	6.4	12	100.0	0	—	—
NE91	10.1	98	2.4	3	—	—	10.7	137
NE93	3.2	32	1.3	73	—	—	5.7	101
NE94	0.7	20	0.3	58	—	—	5.2	38
OH91	8.3	18	13.1	78	26.5	41	—	—
SD92	1.9	31	0.2	39	—	—	10.4	43
WI91	0.3	na	4.1	na	—	—	9.1	na

APPENDIX. Continued.

Site	Pennsylvania smartweed		Wild buckwheat		Yellow foxtail		Hairy nightshade	
	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)
IA93	33.4	20	—	—	—	—	—	—
MN92	0.6	na	—	—	—	—	—	—
MN93	30.6	75	4.7	na	—	—	—	—
MO93	48.5	73	—	—	—	—	—	—
MO94	30.6	58	—	—	—	—	—	—
NE91	—	—	—	—	—	—	1.3	86
NE93	—	—	5.0	48	1.7	163	6.1	39
NE94	—	—	1.8	69	4.2	59	9.3	90
SD92	—	—	0.9	na	5.6	39	—	—
WI91	7.0	na	—	—	—	—	—	—
Site	Tall morning glory		Velvetleaf		Common ragweed		Barnyardgrass	
	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)
MI91	—	—	—	—	6.8	44	—	—
MO93	31.0	22	21.7	4	—	—	—	—
MO94	82.9	20	9.3	19	—	—	—	—
OH91	—	—	—	—	38.2	43	—	—
OH94	—	—	53.4	46	—	—	—	—
SD92	—	—	—	—	0.1	36	58.4	38
Site	Common purslane		Kochia		Wild proso millet		Tansy mustard	
	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)
CO93	—	—	0.3	54	0.6	59	0.0	56
CO94	0	0	50.2	77	3.0	110	0.3	82
NE91	1.4	53	26.6	43	16.1	66	—	—
NE93	41.7	27	—	—	—	—	—	—
Site	Fall panicum		Yellow rocket		Prostrate knotweed		Common sunflower	
	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)
MI91	1.7	95	—	—	—	—	—	—
NE91	—	—	0.0	123	—	—	5.5	20
NE93	—	—	—	—	0	na	6.3	na
NE94	—	—	—	—	1.1	126	—	—
SD92	—	—	—	—	—	—	3.2	na
WI91	—	—	—	—	0.6	na	—	—
Site	Common cocklebur		Prostrate pigweed		Shepard's-purse		Wild mustard	
	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)
MN93	—	—	—	—	—	—	42.8	84
MN94	50.0	12	—	—	—	—	—	—
WI91	—	—	2.8	na	12.0	na	—	—
Site	Spotted spurge		Venice mallow		Yellow woodsorrel		Longspine sandbur	
	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)
IA93	7.5	55	80	na	100	na	—	—
SD92	—	—	—	—	—	—	6.5	58

^a Latin names for species not listed in the abstract are as follows: barnyardgrass, *Echinochloa crus-galli* (L.) Beauv.; common cocklebur, *Xanthium strumarium* L.; fall panicum, *Panicum dichotomiflorum* Michx.; longspine sandbur, *Cenchrus longispinus* (Hack.) Fern.; prostrate pigweed, *Amaranthus blitoides* S. Wats.; shepherd's-purse, *Capsella bursa-pastoris* (L.) Medikus; spotted spurge, *Euphorbia maculata* L.; tall morningglory, *Ipomoea purpurea* (L.) Roth; tansy mustard, *Descurainia pinnata* (Walt.) Britt.; wild mustard, *Sinapis arvensis* L.; venice mallow, *Hibiscus trionum* L.; yellow woodsorrel, *Oxalis stricta* L.